

## FORUM

### From the Phylogeny of the Satyrinae Butterflies to the Systematics of Euptychiina (Lepidoptera: Nymphalidae): History, Progress and Prospects

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#### Abstract

We review the various proposals of evolutionary and classification schemes for Satyrinae and particularly Euptychiina butterflies, assessing progress and prospects of research for the group. Among the highlights is the proposal to include Morphini, Brassolini and Amathusiini as part of Satyrinae. Although it is clear that this hypothesis requires further investigation, phylogenetic studies recently conducted recover this clade as part of Satyrinae with high support. The phylogenetic analyses for Euptychiina carried out to date recover the monophyly of the group and have identified a variety of genera as non-monophyletic. Further work is necessary to resolve the position of the subtribe and the evolutionary relationships of several genera.

#### Introduction

The classification of organisms is an important endeavour in our attempt to understand the diversity of life on this planet (Wilson 2000). A desirable property of classification is that it reflects the evolutionary relationships of the organisms involved, such that names of taxa above the species level define monophyletic groups. This increases the information content of a name and places taxa in an evolutionary context. The advent of molecular systematics has over the past two decades allowed the testing of previous classifications with new forms of data, and indeed has allowed new classifications to be proposed for highly diverse groups of organisms that have previously defied stable classification (e.g. Zahiri *et al* 2011). Here we review the latest studies on the diverse clade of butterflies, Satyrinae, and discuss their implications on the classification of the group, which has been very labile over the past 250 years.

The subfamily Satyrinae, with about 2,500 described species, is one of the most diverse groups of butterflies (Peña & Wahlberg 2008), comprising over a third of the Nymphalidae diversity and found on all continents except Antarctica (Ackery *et al* 1999, DeVries 2000). The group is particularly diverse in the Neotropics, with approximately 1,200 species in 137 genera (Lamas *et al* 2004a), occurring in all habitats with vegetation from sea level to the highlands of the Andes (DeVries 1987).

The host plants of Satyrinae are mostly monocots, with certain eudicot families such as Fabaceae and Menispermaceae being used as well, and some species have been recorded feeding on Lycopodiophyta (Selaginellaceae), Bryophyta (Neckeraceae) and gymnosperms (Cycadaceae) (Singer *et al* 1971, Singer & Mallet 1986, Ackery 1988, Beccaloni *et al* 2008). In general, Satyrinae consume plants that lack secondary chemical compounds, which partly explains the low specificity for their hosts (Murray 2001a). A consequence

of this is that they are mostly palatable organisms (DeVries 1987, but see Rothschild 2001) and are likely to rely mainly on crypsis to avoid predation.

The estimated age of origin of Satyrinae is from 60 to 65 million years (Ma), and their diversification is thought to be influenced by their host plant use (Peña & Wahlberg 2008, Wahlberg *et al* 2009, Peña *et al* 2011). The first Satyrinae evolved in an environment where forests covered most of the land surface and were dominated by dicotyledonous plants (Willis & McElwain 2002). Available monocots were present in the understory, represented by families Arecales, Liliales, Zingiberales and some Poales (Bromeliaceae) (Janssen & Bremer 2004, Linder & Rudall 2005). Diversification of the most species-rich tribe of Satyrinae, Satyrini, is linked to the radiation of the Poaceae (36-23 Ma), which was a determinant factor of the diversity of the tribe (Peña & Wahlberg 2008). Subtribes such as Euptychiina and Pronophilina, which together include more than 1,000 described species (Lamas 2004a, Lamas *et al* 2004b), are a good example of the impact that the Poaceae radiation had on the Satyrini diversification, where the majority of plant species used as hosts are found (DeVries 1987, Murray 2001ab, Viloría 2003).

The adults of most Satyrinae species are diurnal with low dispersal abilities, flying near the ground, preferably in shaded areas of the forest (understory), feeding on fruits in various stages of decomposition and associated fungi (DeVries 1987, Kremen 1994, Viloría 1998, Murray 2001a). Due to their biology, diversity and distribution, Satyrinae is a dominant group in most communities of butterflies (DeVries 1994, DeVries *et al* 1997, Brown & Freitas 2000, 2002, Pyrcz & Wojtusiak 2002, Tobar *et al* 2002, Ribeiro *et al* 2008, Vu 2009). The subfamily has species that exhibit special affinity for certain types of vegetation as open areas, primary or secondary forest (DeVries *et al* 1997), being considered useful indicators of ecosystem characteristics (Kremen 1992, 1994, Uehara-Prado *et al* 2007) and used in population studies (Vila & Björklund 2004, Schmitt *et al* 2005, Besold *et al* 2008) and conservation biology (Dennis & Eales 1997, Bergman 1999).

The great diversity of Satyrinae, both in species richness as well as morphology, has meant that there has been great uncertainty and taxonomic difficulties in classifying these butterflies. Until recently, there was no consensus regarding their phylogeny and classification (Viloría 1998, 2003, Lamas *et al* 2004a, Peña *et al* 2006, 2011). Thus, priority areas of study required for advancing the knowledge of their biological and evolutionary aspects need to be identified. This work summarizes the recent evolutionary proposals for Satyrinae, particularly for the Euptychiina, reviewing evidence from various studies and providing guidance for the development of further investigations on the group.

## Satyrinae in Nymphalidae

The most accepted classification of Nymphalidae was proposed by Ackery *et al* (1999), which is based mainly on the evolutionary relationships suggested by de Jong *et al* (1996) and the classification of Harvey (1991). In these, as in most other studies, the taxonomic status of Satyrinae remains stable, but their evolutionary relationships with other subfamilies are contested and only agree on the position of Satyrinae being closely related to Morphinae *sensu* Ackery *et al* (1999) (Ehrlich 1958, Ehrlich & Ehrlich 1967, Miller 1968, Ackery 1984, DeVries *et al* 1985, Scott 1985, Martin & Pashley 1992, Weller *et al* 1996).

Phylogenetic relationships among Satyrinae and Morphinae *sensu* Ackery *et al* (1999) are reviewed by recent studies that improved our understanding of the group's position. These studies have used both morphological (Freitas & Brown 2004) and molecular characters (Brower 2000, Wahlberg *et al* 2003, Peña *et al* 2006) to find further support for clades, and more recently employing a total evidence approach in order to obtain more consistent and coherent hypotheses (Wahlberg *et al* 2005, 2009, Peña & Wahlberg 2008). These studies yielded similar results with morphological characters of adults and immatures (Freitas & Brown 2004) and with DNA sequences of mitochondrial (COI) and nuclear (EF-1 $\alpha$  and wingless) (Brower 2000, Wahlberg *et al* 2003) genes, finding a "satyroid" clade made up of Charaxinae, Calinaginae, Satyrinae and Morphinae. Also, combining morphological characters of adults and molecular data provides further support for this clade (Wahlberg *et al* 2005), but its relationship to the rest of Nymphalidae remains unresolved.

The lack of resolution within the "satyroid" clade can be attributed to taxonomic sampling, *i.e.*, due to not including a number of taxa in proportion to the diversity of the clade, causing long branch attraction artifacts that affect the resulting topology and stability of the nodes (Poe 1998, Hedtke *et al* 2006, Heath *et al* 2008a). This problem is compounded by the presence of variations in rates of speciation and extinction among taxa, producing unbalanced topologies, where limited taxonomic sampling causes a greater loss of balance in the resulting tree (Heath *et al* 2008b). This situation occurs due to the diversification of Satyrinae (Satyrini in particular), which is linked to the radiation of Poaceae (36-23 Ma) (Peña & Wahlberg 2008, Peña *et al* 2011), and probably has higher speciation rates than the rest of Nymphalidae.

Seeking to reduce the effect of attraction of long branches and with the aim of obtaining a more robust phylogenetic proposal, Peña *et al* (2006) conducted a sampling of 191 taxa using characters of the mitochondrial gene COI and the nuclear genes EF-1 $\alpha$  and wingless. These authors assessed mainly the monophyly of Satyrinae and relations among their tribes and subtribes, finding

a solid support for the clade comprised of Satyrinae and Morphinae (Morphini, Brassolini and Amathusiini). The Satyrinae, as conceived by the traditional classification (Ackery *et al* 1999), appeared as a paraphyletic assemblage also including Morphinae tribes, suggesting that these tribes should be placed within Satyrinae.

These results are also supported by Peña & Wahlberg (2008) and Wahlberg *et al* (2009). The latter study used a combination of 235 morphological characters and 10 nuclear and mitochondrial genes in 400 genera of Nymphalidae (75% of the total generic diversity). The results establish a “satyroid” clade made up of Calinaginae, Charaxinae and Satyrinae, where Calinaginae is the sister group of Charaxinae + Satyrinae. Morphinae *sensu* Ackery *et al* (1999) emerges as an unnatural group, with the tribes Morphini, Brassolini and Amathusiini grouped within Satyrinae (Fig 1). Thus, with this delineation of Satyrinae, the subfamily is recovered as a monophyletic group and its taxonomic position and evolutionary relationships with other subfamilies of the group are clear.

**Evolutionary Relationships within Satyrinae**

Satyrinae has complex relations among its groups, some being cohesive (tribes and subtribes), structured and others poorly defined. According to the schemes proposed by Peña *et al* (2006, 2011), Peña & Wahlberg

(2008) and Wahlberg *et al* (2009) (Fig 1), the subfamily includes four well defined groups: 1) the two Neotropical clades (Morphini + Brassolini), 2) the clade [Elymniini + Amathusiini + Zetherini + (Dirini + Melanitini)], 3) the clade including the Neotropical Haeterini, and 4) the speciose Satyrini. Taking into account these clades, Satyrinae could include nine tribes and 16 subtribes (Table 1), although several of these groups have received little attention, and do not have clear and more definitive studies to assess their position and taxonomic status.

The Morphini + Brassolini clade was initially recognized by Ehrlich (1958) and Ehrlich & Ehrlich (1967) and treated as the subfamily Morphinae, until Miller (1968) included most of its members [Brassolini and Antirrheina (Morphini)] within Satyrinae. Later studies resurrected Morphini + Brassolini (including Biina) (DeVries *et al* 1985, Ackery *et al* 1999, Vane-Wright & Boppré 2004) and the clade is currently considered as one of the most stable within Satyrinae, being supported by molecular and morphological characters (Peña *et al* 2006, Peña & Wahlberg 2008, Wahlberg *et al* 2009).

The clade composed by Melanitini, Dirini, Amathusiini, Zetherini and Elymniini, of almost exclusively Palearctic distribution, has been recovered by various studies, but the deeper relationships remain unresolved. The most stable group is composed by the Old World Melanitini + Dirini, which is recovered in all studies (Peña *et al* 2006, Peña & Wahlberg 2008, Wahlberg *et al* 2009, Price *et al* 2010), with both tribes being well-defined

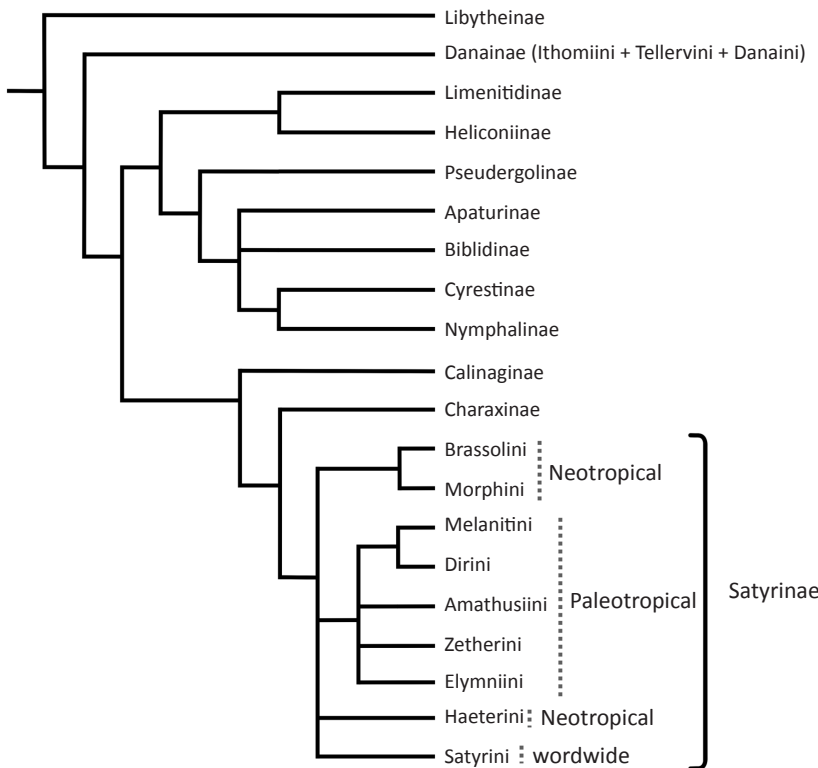


Fig 1 Consensus of hypotheses showing the phylogenetic position of Satyrinae in Nymphalidae, relationships of tribes (according to Peña *et al* 2006, Peña & Wahlberg 2008, Wahlberg *et al* 2009) and their distribution.

Table 1 Different classification proposals for Satyrinae.

Miller (1968)	Harvey (1991)	Recent results <sup>1</sup>
Satyridae	Satyrinae	Satyrinae
Haeterinae	Haeterini	Morphini
Haterini	Biini	Antirrheina
Brassolinae	Melanititi	Morphina
Brassolini	Biiti	Brassolini
Biinae	Eritini	Biina
Melanitini	Ragadiini	Brassolina
Antirrhini	Elymniini	Naropina
Biini	Elymniiti	Elymniini
Elymniinae	Lethiti	Amathusiini
Elymniini	Mycalesiti	Zetherini
Lethini	Zetheriti	Dirini
Mycalesini	Satyrini	Melanitini
Zetherini	Hypocystiti	Haeterini
Eritinae	Ypthimiti	Satyrini
Eritini	Euptychiiti	Parargina
Ragadiinae	Coenonymphiti	Lethina
Ragadiini	Manioliti	Mycalesina
Satyrinae	Erebiiti	Coenonymphina
Hypocystini	Pronophiliti	Eritina
Ypthimini	Melanargiiti	Ragadiina
Euptychiini	Satyriti	Euptychiina
Coenonymphini		Ypthimina
Manioloni		Melanargiina
Erebiini		Maniolina
Pronophilini		Pronophilina
Melanargiini		Erebiina
Satyrini		Satyrina

<sup>1</sup>Consensus resulting from Kodandaramaiah *et al* (2010a), Penz (2007), Peña *et al* (2006), Peña & Wahlberg (2008), Peña *et al* (2011) and Wahlberg *et al* (2009).

morphologically. The exception is *Manataria*, the only genus in the clade with a Neotropical distribution, which in some cases appears as sister to Melanitini and other times to Dirini.

The evolutionary relationships of Amathusiini, Zetherini and Elymniini within the clade are not yet resolved. The tribes Amathusiini (without *Hyantis* and *Xanthotaenia*) and Zetherini appear well supported, but Elymniini (comprising only *Elymnias*) is grouped with different tribes in different studies: with Haeterini (fig 7 in Peña *et al* 2006), Amathusiini (fig 1 in Peña & Wahlberg 2008, and Wahlberg *et al* 2009) and Melanitini + Dirini (fig 3s in Wahlberg *et al* 2009). The genus *Xanthotaenia*

is sister to the tribe Zetherini with strong support, and should be transferred to that tribe. The position of *Hyantis* (and the putatively related *Morphopsis*), a genus traditionally placed in Amathusiini, seems uncertain as it is not supported as part of this tribe and in some cases appears to be related with Elymniini (fig 3s in Wahlberg *et al* 2009) or the clade Dirini + Melanitini (Peña & Wahlberg 2008). Clearly this clade of butterflies requires further work to resolve relationships of the taxa comprising it.

Haeterini is a small group of Neotropical distribution consisting of 21 species and five genera (Lamas 2004b). Although well supported, its phylogenetic position is ambiguous. Miller (1968) placed the Haeterini as the sister of all other Satyrinae. In recent studies, however, this group appeared as sister to Satyrini (Peña & Wahlberg 2008) or to the clade ((Melanitini + Dirini) + Amathusiini + Zetherini + Elymniini) (fig 3s in Wahlberg *et al* 2009).

The tribe Satyrini is the most diverse of the subfamily, comprising over 80% of the species, distributed in five continents. This clade is recovered in various phylogenetic studies (Peña *et al* 2006, 2011, Peña & Wahlberg 2008, Wahlberg *et al* 2009) with partially resolved relationships and only supported by molecular characters (Fig 2) [(Peña *et al* 2006, 2011, Peña & Wahlberg 2008 (their fig 1), Wahlberg *et al* 2009 (their figs 1 and 3s), Kodandaramaiah *et al* 2010a)].

The lack of resolution in the topology of Satyrini is

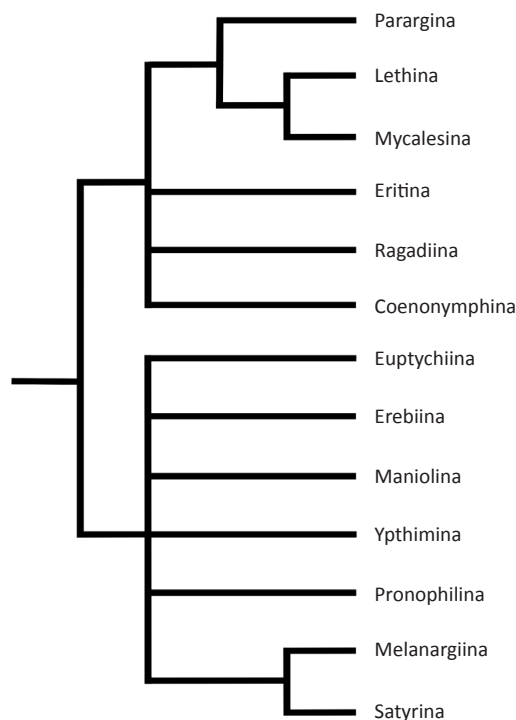


Fig 2 Consensus of the hypotheses of phylogenetic relationships among the subtribes of Satyrini (according to Kodandaramaiah *et al* 2010a, Peña *et al* 2006, 2011, Peña & Wahlberg 2008, Wahlberg *et al* 2009).

most likely due to the rapid radiation of the group (Pena & Wahlberg 2008, Peña *et al* 2011) that produces a combination of long and short branches causing branch attraction problems and creates an artifact between the outgroup and ingroup, making it difficult to recover the monophyly of the entire group (Shavit *et al* 2007, Whitfield *et al* 2007).

This phenomenon occurs in most of the subtribes of Satyrini (Peña *et al* 2011) and has been recently reported in Coenonymphina (Kodandaramaiah *et al* 2010a), Euptychiina (Peña *et al* 2010) and Mycalesina (Kodandaramaiah *et al* 2010b). Peña *et al* (2011) find that the initial selection of Haeterini as outgroup for Satyrini produces unstable trees where *Euptychia* (Euptychiina) appears outside of Satyrini. This problem was solved with an improved taxonomic sampling in the outgroup level with the inclusion of several Morphini (rooting with *Morpho*) and Brassolini. This managed to break the branch attraction that Haterini produced with the long terminal branch of the ingroup (*Euptychia*) recovering Satyrini as a monophyletic group.

In a study on Coenonymphina, Kodandaramaiah *et al* (2010a) established that the ingroup relationships can be affected by changes in sampling density in combination with the outgroup taxa selected, finding that the effect of the outgroup is more pronounced in the basal nodes (Kodandaramaiah *et al* 2010a, Peña *et al* 2011). Thus, proper selection of outgroups can reduce the traction between them and the genera near the basal nodes, allowing to recover the monophyly of the group.

Satyrini is divided into two major clades. One clade includes Coenonymphina + Ragadiina + Eritina + [Parargina + (Mycalesina + Lethina)], with Coenonymphina represented by the genera that Miller (1968) placed in his Coenonymphini, Hypocystini and the genus *Oressinoma* (Euptychiini). The position of Ragadiina within the clade is complex, appearing polyphyletic, with *Ragadia* as the sister group of Eritina, while *Acrophtalmia* forms a clade with *Loxerebia* and *Coelites* (Peña *et al* 2011), a result that requires further study as these genera are poorly represented in phylogenetic studies conducted to date.

The other clade is composed by the tribes Euptychiina + Ypthimina + (Melanargiina + Satyrina) + Maniolina + Pronophilina + Erebiina, with poorly resolved internal relationships. Ypthimina appears as a monophyletic group that includes the genera that Miller (1968) located in *Ypthima*-series and *Melampias*-series, however the genera belonging to the *Callerebia*-series seem not to belong to Ypthimina, sampled genera include *Loxerebia*, *Callerebia* and *Paralasa*, which are located in different parts of the phylogeny of Satyrini (Peña *et al* 2011).

The Neotropical Pronophilina is one of the most diverse groups of butterflies with complex phylogenetic relationships, reflected in the classification of Lamas & Vitoria (2004a) and Lamas *et al* (2004b). In this

classification, the genera that Miller (1968) grouped in Pronophilina are divided into three subtribes, Hypocystina (now Coenonymphina), Erebiina and Pronophilina. This proposal arose from the phylogenetic study by Vitoria (1998, 2003, 2007), which was based on morphological characteristics of adults, and reported a close relationship of the Neotropical genera of Pronophilina with Australian Coenonymphina and Paelearctic Erebiina.

The phylogeny proposed by Vitoria (1998, 2003, 2007) recovered Pronophilina *sensu* Miller (1968) largely as a non-monophyletic group, with most of the genera organized in two clades largely agreeing with the classification proposed by Lamas *et al* (2004b). The first clade is composed mostly by what he called the "Neotropical Coenonymphina and Erebiina", and the second clade corresponds to the Pronophilina *sensu stricto*. However, recent comprehensive studies (Peña *et al* 2006, 2011, Wahlberg *et al* 2009) recovered the two clades as sister groups which are not related to the Old World Coenonymphina and Erebiina. Thus, it appears that the classification proposed by Lamas *et al* (2004b) and Lamas & Vitoria (2004a) should be reverted back to the one proposed by Miller (1968).

The phylogenetic relationships within Pronophilina continue to be a complex issue. The studies of Peña *et al* (2006, 2011) and Wahlberg *et al* (2009) did not recover the complete monophyly of the group, with *Calisto* and *Eretris*, two genera traditionally treated as part of Pronophilina, appearing outside this clade, probably as an artifact of long branch attraction (Peña *et al* 2011). There is a clear need for further phylogenetic studies that involve large taxonomic sampling and employing a large number of molecular and morphological characters. Assessing the monophyly of the subtribes of Satyrini is a priority in order to obtain more robust phylogenetic proposals for the group.

### Phylogenetic Relationships and Classification of Euptychiina

Euptychiina is a very diverse group of Satyrinae, with over 400 recognized species (Lamas 2004a) in 44 genera (Table 2, Fig 3) (Peña *et al* 2010). The group is distributed mainly in the Neotropical region, with the presence of some species in the Nearctic region and one in Southeast Asia. They are found from sea level to 3,500 m.a.s.l., although the largest species richness occurs in the lowlands (DeVries 1994, DeVries *et al* 1997, Brown & Freitas 2002, Tobar *et al* 2002, Ribeiro *et al* 2008).

The taxonomy of the group is among the most poorly known of all Neotropical butterflies because of their high diversity and the morphological homogeneity of its members (Peña & Lamas 2005). There is a large number of species to be described (*e.g.* in *Caeruleuptychia*,

Table 2 Different proposed classifications of Euptychiina.

Miller (1968)	Lamas (2004b)	Peña <i>et al</i> (2010)
<i>Archeuptychia</i> Forster	<i>Archeuptychia</i> Forster	<i>Amphidecta</i> Butler
<i>Caeruleuptychia</i> Forster	<i>Caenoptychia</i> Le, Cerf	<i>Archeuptychia</i> Forster
<i>Capronniera</i> Forster	<i>Caeruleuptychia</i> Forster	<i>Caenoptychia</i> Le, Cerf
<i>Cepheuptychia</i> Forster	<i>Capronniera</i> Forster	<i>Caeruleuptychia</i> Forster
<i>Chloreuptychia</i> Forster	<i>Cepheuptychia</i> Forster	<i>Capronniera</i> Forster
<i>Cissia</i> Doubleday	<i>Cercyeuptychia</i> Miller & Emmel	<i>Cepheuptychia</i> Forster
<i>Coeruleotaygetis</i> Forster	<i>Chloreuptychia</i> Forster	<i>Cercyeuptychia</i> Miller & Emmel
<i>Cyllopsis</i> Felder	<i>Cissia</i> Doubleday	<i>Chloreuptychia</i> Forster
<i>Erichthodes</i> Forster	<i>Coeruleotaygetis</i> Forster	<i>Cissia</i> Doubleday
<i>Euptychia</i> Hübner	<i>Cyllopsis</i> Felder	<i>Coeruleotaygetis</i> Forster
<i>Euptychoides</i> Forster	<i>Erichthodes</i> Forster	<i>Cyllopsis</i> Felder
<i>Godartiana</i> Forster	<i>Euptychia</i> Hübner	<i>Erichthodes</i> Forster
<i>Harjesia</i> Forster	<i>Euptychoides</i> Forster	<i>Euptychia</i> Hübner
<i>Haywardiana</i> Forster	<i>Forsterinaria</i> Gray	<i>Euptychoides</i> Forster
<i>Hermeuptychia</i> Forster	<i>Godartiana</i> Forster	<i>Forsterinaria</i> Gray
<i>Magneuptychia</i> Forster	<i>Harjesia</i> Forster	<i>Godartiana</i> Forster
<i>Megeuptychia</i> Forster	<i>Hermeuptychia</i> Forster	<i>Guaianaza</i> Freitas & Peña
<i>Megisto</i> Hübner	<i>Magneuptychia</i> Forster	<i>Harjesia</i> Forster
<i>Moneuptychia</i> Forster	<i>Megeuptychia</i> Forster	<i>Hermeuptychia</i> Forster
<i>Neonympha</i> Hübner	<i>Megisto</i> Hübner	<i>Magneuptychia</i> Forster
<i>Oressinoma</i> Doubleday	<i>Moneuptychia</i> Forster	<i>Megeuptychia</i> Forster
<i>Paramacera</i> Butler	<i>Oressinoma</i> Doubleday	<i>Megisto</i> Hübner
<i>Parataygetis</i> Forster	<i>Paramacera</i> Butler	<i>Moneuptychia</i> Forster
<i>Pareuptychia</i> Forster	<i>Parataygetis</i> Forster	<i>Neonympha</i> Hübner
<i>Paryphthimoides</i> Forster	<i>Pareuptychia</i> Forster	<i>Palaeonympha</i> Butler
<i>Pharneuptychia</i> Forster	<i>Paryphthimoides</i> Forster	<i>Paramacera</i> Butler
<i>Pindis</i> Felder	<i>Pharneuptychia</i> Forster	<i>Parataygetis</i> Forster
<i>Posttaygetis</i> Forster	<i>Pindis</i> Felder	<i>Pareuptychia</i> Forster
<i>Praefaunula</i> Forster	<i>Posttaygetis</i> Forster	<i>Paryphthimoides</i> Forster
<i>Pseudeuptychia</i> Forster	<i>Praefaunula</i> Forster	<i>Pharneuptychia</i> Forster
<i>Pseudodebis</i> Forster	<i>Pseudeuptychia</i> Forster	<i>Pindis</i> Felder
<i>Rareuptychia</i> Forster	<i>Pseudodebis</i> Forster	<i>Posttaygetis</i> Forster
<i>Satyrotaygetis</i> Forster	<i>Rareuptychia</i> Forster	<i>Praefaunula</i> Forster
<i>Splendeuptychia</i> Forster	<i>Satyrotaygetis</i> Forster	<i>Pseudeuptychia</i> Forster
<i>Taygetina</i> Forster	<i>Splendeuptychia</i> Forster	<i>Pseudodebis</i> Forster
<i>Taygetis</i> Forster	<i>Taydebis</i> Freitas	<i>Rareuptychia</i> Forster
<i>Vareuptychia</i> Forster	<i>Taygetina</i> Forster	<i>Satyrotaygetis</i> Forster
<i>Weymerana</i> Forster	<i>Taygetis</i> Hübner	<i>Splendeuptychia</i> Forster
<i>Yphtimoides</i> Forster	<i>Taygetomorpha</i> Miller	<i>Taydebis</i> Freitas
<i>Zischkaia</i> Forster	<i>Yphtimoides</i> Forster	<i>Taygetina</i> Forster
	<i>Zischkaia</i> Forster	<i>Taygetis</i> Hübner
		<i>Taygetomorpha</i> Miller
		<i>Yphtimoides</i> Forster
		<i>Zischkaia</i> Forster



Fig 3 A pout-pourri of Euptychiina diversity (all in ventral view): 1) *Cepheuptychia cephus*, 2) *Chloreuptychia arnaca*, 3) *Cissia similis*, 4) *Euptychoides griphe*, 5) *Euptychia enyo*, 6) *Forsterinaria boliviana*, 7) *Hermeuptychia pompilia*, 8) *Magneuptychia tricolor*, 9) *Megisto cymela*, 10) *Moneuptychia paeon*, 11) *Paramacera xicaque*, 12) *Splendeuptychia boliviensis*, 13) *Pareuptychia hesionides*, 14) *Palaeonympha opalina*, 15) *Taygetis thamyra*, 16) *Taygetomorpha celia*, 17) *Ypthimoides* sp., 18) *Zischkaia pacarus*.

*Euptychia*, *Magneuptychia* and *Splendeuptychia*), making clear the importance of detailed taxonomic work in the group.

Most Euptychiina genera were described by Forster (1964), based on specimens from Bolivia. In that work, Forster described a total of 33 genera, although he did not provide detailed descriptions or diagnostic characteristics for them, and also did not include many species from other regions of the Neotropics. Forster's results were taken into account by Miller (1968) in his proposal for the classification of Euptychiina (Table 2), but it has been ignored by many authors, who have preferred to use *Euptychia* in a broad sense or just considered the genera described prior to the work of Forster (DeVries 1987, D'Abrera 1988). Recently, Lamas (2004a), following the classification of Miller (1968), retained most of the genera proposed by Forster (1964) and included several additional genera (*Cercyeuptychia*, *Caenoptychia*, *Taydebis* and *Taygetomorpha*) (Table 2). Although this scheme is still lacking evolutionary support, it is now widely accepted and is taken as a baseline for conducting further studies in this group.

Investigations conducted so far that have looked at phylogenetic relationships in Euptychiina used DNA sequences of mitochondrial (COI, Cytb and ND1) and nuclear genes (EF-1 $\alpha$ , wingless, GAPDH and RpS5) (Murray & Prowell 2005, Peña *et al* 2006, 2010, Marín *et al* 2009), as well as characters of immature morphology (Murray 2001a). Although the results of Murray (2001a) have not been formally published, they provide important information on immature stages for further investigations on the group.

The proposed phylogenies of Murray & Prowell (2005) and Peña *et al* (2006, 2010) show that Euptychiina *sensu* Lamas (2004a) is not a monophyletic taxon. Some genera previously regarded as *incertae sedis*, such as *Amphidecta* and *Palaeonympha*, are now included in Euptychiina, and *Oressinoma*, a genus traditionally recognized as a member of Euptychiina, is more closely related to Coenonymphina (Peña *et al* 2006).

The research on Euptychiina has struggled to show the monophyly of the group (Murray & Prowell 2005, Peña *et al* 2010). Again, it is believed that this is caused by problems of long branch attraction, particularly in *Euptychia* (Peña *et al* 2011), which is recognized as the sister group of the remaining members of the subtribe (Peña *et al* 2006, 2010). For this genus, it is established that, after diverging from the original lineage, species underwent rapid evolutionary changes, resulting in spurious grouping with other long branches of Satyrini (Peña *et al* 2011).

Within the subtribe, the evolutionary reconstruction proposed shows three (Murray & Prowell 2005) to five clades  $\{[Megisto + (Hermeuptychia + [(Pareuptychia + Taygetis + Splendeuptychia])]\}$  (Peña *et al* 2010), with

some well defined groups and others that appear to be unnatural taxonomic units (Murray 2001a, Murray & Prowell 2005, Peña *et al* 2010).

The *Megisto* group proposed by Peña *et al* (2010) was not recovered in previous studies, probably due to a lower taxonomic sampling, although similar groups were recovered (Murray & Prowell 2005, Peña *et al* 2006). This group is found to be sister to the rest of Euptychiina and consists of the genera  $\{[Palaeonympha + Megisto + [Cissia + (Moneuptychia + Yphthimoides)]]\}$ . The first two genera are of North America and Southeast Asia distribution, *Cissia* is widely distributed in the Neotropical region and is particularly diverse in Central America and Northern Andes and appears as the sister group of *Yphthimoides* + *Moneuptychia*, both highly diversified in Southeast Brazil.

Recent results suggest a North American origin of *Palaeonympha*, a genus that shares several morphological characters with *Megisto* (Miller 1968), giving support to the proposed biogeographic scenario of Peña *et al* (2010), in which *Palaeonympha* ancestors crossed the Asian continent by the Bering Strait and settled in Southeast Asia.

*Cissia* is always recovered as a polyphyletic group, with their members spread in the clades *Splendeuptychia* and *Megisto* (Murray & Prowell 2005, Peña *et al* 2010). In the group *Yphthimoides* + *Moneuptychia* (Peña *et al* 2010), *Yphthimoides* is recovered as monophyletic, even though taxonomic sampling is still unsatisfactory and has not included the type species, *Y. yphthima* (C Felder & R Felder). For *Moneuptychia*, the species are split into two clades, one composed by *M. paeon* (Godart) and *M. griseldis* (Weymer) and related to *Yphthimoides*, and a second composed by *M. itapeva* Freitas, *Pharneuptychia* sp., *Euptychoides castrensis* (Shaus), *M. giffordi* Freitas *et al* and *M. soter* (Butler), the latter being the type species of the genus (Freitas 2007, Freitas *et al* 2010, Peña *et al* 2010).

The *Hermeuptychia* clade consists of *Hermeuptychia* and several taxa that were previously considered *incertae sedis*. It is the most widely distributed group of Euptychiina, found from northern Argentina to southern United States, occurring from sea level to about 3,000 meters above sea level (DeVries 1987). This clade is recovered as monophyletic in all published studies so far (Murray & Prowell 2005, Marín *et al* 2009, Peña *et al* 2010). However, *Hermeuptychia* includes a complex of cryptic species of undefined phylogenetic relationships (Marín *et al* 2009).

Peña *et al* (2010), with increased taxonomic sampling, found the sister group of *Hermeuptychia* to be the clade formed by  $[Rareuptychia\ clio\ (Weymer) + (Amphidecta\ calliomma\ (C.\ Felder\ \&\ R.\ Felder) + Euptychia\ ordinata\ (Weymer)]$ , the latter two species treated as *incertae sedis* by Lamas (2004b). The genus *Amphidecta*, previously



treated as part of Pronophilina (Miller 1968) and as *incertae sedis* by Lamas & Vilorio (2004b), has been finally included in Euptychiina by Peña *et al* (2006).

The *Taygetis* clade is the most stable group within Euptychiina, being recovered in all known studies (Murray & Prowell 2005, Peña *et al* 2006, 2010, Marín *et al* 2009). Two main groups can be recognized in this clade, the first composed by *Forsterinaria* + *Harjesia blanda* (Möschler) + *Parataygetis* + *Guaianaza* + *Posttaygetis*, and the second composed by *Pseudodebis* + *Taygetis* + *Taygetomorpha* + *Harjesia oreba* (Butler). In the first group, *Forsterinaria* is paraphyletic in relation to *Guaianaza*, and the validity of the former genus should be revised. In the second group, *Taygetis* appears, as a non-monophyletic taxon, in two separate clades, showing that there is a need for a revision of this genus.

The *Pareuptychia* clade consists of *Satyrotaygetis satyrina* (H. W. Bates), *Neonympha aerolatus* (Smith), *Taydebis peculiaris* (Butler), *Splendeuptychia doxes* (Godart), *Splendeuptychia furina* (Hewitson) and of the genera *Pareuptychia*, *Megeuptychia* and *Erichthodes* (Murray & Prowell 2005, Peña *et al* 2010). The sister group of the *Pareuptychia* clade is formed by *Chloreuptychia* + *Cepheuptychia cephus* (Fabricius) + *Archeuptychia*. Although this is a clade with high support, its internal phylogenetic relationships are poorly defined. The genus *Chloreuptychia* is clearly polyphyletic, with their members divided into two distinct clades, and by including *Archeuptychia* and *Cepheuptychia* within it.

Finally, the *Splendeuptychia* clade is a group composed of several poorly defined genera, with the exception of *Caeruleuptychia*, which is recovered as a monophyletic group. Currently, *Splendeuptychia*, *Magneuptychia* and *Cissia* are recovered as polyphyletic or paraphyletic groups, being indicative of the complex taxonomic problems of this group (Murray & Prowell 2005, Peña *et al* 2010).

In addition to the clades discussed above, there are a number of taxa that do not form clearly defined groups, and whose phylogenetic position remains unclear. Among these taxa we can highlight (*Cercyeuptychia* + *Godartiana*) + [*Chloreuptychia catharina* (Staudinger) + *Pindis*] and a clade consisting of *Zischkaia*, *Pharneuptychia innocentia* (C. Felder & R. Felder), *Splendeuptychia boliviensis* and *S. itonis* (Peña *et al* 2010). More data will be required to elucidate the phylogenetic relationships of these taxa.

To summarize, several Euptychiina genera are polyphyletic, with species being recovered scattered in different lineages as inferred by different phylogenetic proposals of the subtribe (Murray & Prowell 2005, Peña *et al* 2010). This is the situation of *Euptychoides*, *Cissia*, *Splendeuptychia*, *Chloreuptychia*, *Harjesia* and *Paryphthimoides*, which are thus of possible artificial composition and need to be revised. In addition, several genera are paraphyletic, such as *Taygetis*, *Pseudodebis*,

*Forsterinaria*, *Magneuptychia* and *Moneuptychia*. These results show that Euptychiina is a group with taxonomic problems with some incorrectly defined genera of paraphyletic or polyphyletic composition and presence of complex species, making identification difficult at this level.

### Are Stable Classifications Attainable?

The use of molecular characters has been crucial to the resolution of phylogenetic relationships in the subfamily Satyrinae. Certain clades, such as Morphini and Haeterini, have long been well characterized by morphological characters, yet their positions within Satyrinae, or indeed Nymphalidae, have been controversial as previously discussed. Molecular characters have the advantage that their numbers can be increased almost without limit, and phylogenetic hypotheses derived using them can be informative about the evolution of morphological characters. Morphological characters on the other hand are still very necessary to visually categorize specimens in the field and in museum collections. Molecular means of identifying specimens to species or higher taxa will never replace visual inspection of them, and can be seen as a complementary method to the traditional methods (see discussion in Silva-Brandão *et al* 2009).

As our review of the studies of Satyrinae has shown, molecular methods have allowed robust testing of proposed classifications of the group. Many proposed classifications can be rejected based on the results and new, unexpected, relationships have been uncovered. The amount of data used (up to 10 gene regions) or taxa sequenced (up to 90% of all extant species for some higher taxa) has cleared many questions, but has also left many questions unanswered, as well as raised new questions. Clearly much more work is necessary to arrive at a stable classification for all species in Satyrinae, yet the work so far has suggested a stable higher classification for the subfamily.

An advantage of the Linnean hierarchical system is that all clades do not need to be named, and thus unstable clades need not be placed in a formal classification. Our review on Satyrinae is a case in point, as we are able to place almost all species in higher taxa, such as subfamily, tribe and subtribe, which are stable and robust to the addition of data, even though the relationships of some taxa are not stable. For example, the position of Euptychiina within Satyrini is not stable, but it is without question within the larger clade Satyrini, and not e.g. in Morphini. The classification thus remains stable, even if the position of Euptychiina changes within Satyrini. It is the search for such stable clades that should drive the studies on the higher classification of life. Such thoughts are not entirely relevant to the species level, as different

processes are acting on populations and the course of evolutionary history is still in the running, whereas in higher taxonomic groups, one can consider that what happened, happened and we are simply trying to uncover that history.

## Conclusions

The phylogenetic proposals of Peña *et al* (2006), and especially those of Wahlberg *et al* (2009), give light on the situation and phylogenetic position of Satyrinae, solving in part the evolutionary relationships of this subfamily and its tribes. Likewise, these studies demonstrate the importance of an appropriate taxonomic sampling and the usefulness of exploring both the morphological and molecular characters for obtaining stronger evolutionary hypothesis. These studies leave the door open for future research on each of the tribes of Satyrinae and show the need of a biogeographic analysis to evaluate the hypothesis proposed by Miller (1968). The latter seems to be corroborated in part by current assumptions.

In Euptychiina, it is necessary to conduct phylogenetic studies that employ ecological or morphological characters to complement the work done with molecular and morphological characters of immature stages (Murray & Prowell 2005, Peña *et al* 2006, 2010, Marín *et al* 2009). This work has helped to resolve the monophyly of the group, but still has problems and ambiguities. The inclusion of other characters can bring information to the solution of these problems. It will be possible to identify morphological synapomorphies that define genera and other clades, which is needed to properly classify the new species that still remain to be described.

Within the subtribe, it is necessary to perform phylogenetic studies focused on clades that have some support (*Megisto*, *Hermeuptychia*, *Taygetis*, *Pareuptychia* and *Splendeuptychia*), allowing more detailed analyses, particularly of the most diverse genera. This work should continue with the revision of various Euptychiina genera, giving priority to *Splendeuptychia*, *Paryphthimoides*, *Euptychoides*, *Euptychia*, *Magneuptychia*, *Cissia* and *Chloreuptychia*, which are paraphyletic or polyphyletic, covering much of the diversity of the tribe.

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